25.

Variations in the Nesting Habits of *Ameiurus nebulosus* (Le Sueur).

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(Plates I & II; Text-figures 1-3).

Introduction.

A study of the reproductive habits of *Ameiurus nebulosus* (Le Sueur) based on aquarium observations together with comments on nematognath reproduction in general was made the subject of an earlier communication in this journal, Breder (1935). The present paper represents the results of further studies on the same species made under less restricted conditions, with special reference to interactions between parents and young and between adjacent family groups.

For purposes of this study and others a pool was constructed on the author's property at Mahwah, N. J. The general configuration is shown in Text-figure 1 and was arrived at partly by following the general contours of the land with fairly proportionate increases in depth. As wide a variety of environmental conditions as possible, within its limitations, was provided. The pool was lined with concrete as the sandy nature of the soil (glacial till) precluded the formation of any permanent standing water. Water is supplied from the house piping to an inlet brooklet at the southwest corner of the pool. To all intents and purposes this is to say it is spring fed, since the water supply is obtained, untreated, from a natural spring about one-half mile distant. This water is very soft, has a pH of about 7.0 and is exceptionally clear. The pool is not continually fed but simply enough is added from time to time to make up for evaporation, which may be considerable in mid-summer.

The pool was built and filled with water on June 26, 1937, and has not since been drained. In previous years it was used for other fishes. The bottom has a covering of leaves from the previous seasons which overlay a bedding of sand in some places providing a very satisfactory pond bottom which is now well seasoned and inhabited by a large number of aquatic invertebrates which in one way or another have become established. They include such forms as *Physa, Asellus,* hydracarinids and many of the winged aquatic insects, such as *Dytiscus, Hydrophilus* and the nymphs of various Odonata. The open water and surface is inhabited by *Corixia, Notonecta, Gyrinus* and *Gerris.* Mosquito larvae have apparently been kept in complete check by the fishes.

The only vertebrates that have established themselves are frogs, including *Rana catesbeiana* and *R. clamitans. Hyla crucifer* and *Bufo americanus* are there in season and occasionally a wandering *R. palustris* puts in an appearance.

At the time the catfish were introduced the only planted animal organisms consisted of a small school of *Rhodeus amarus* and a few *Unio complanatus* which had wintered over from the preceding year.

Since this pool has not been disturbed since originally established it has arrived at a more or less balanced state and the water is usually of such clarity as to be excellent for observational purposes.

Into this setting six catfish were placed on April 26, 1939, in the hope that at least one mating would result. These fish were supplied through the good services of Mr. W. C. Bennett, Engineer of the New York Aquarium, who had obtained them from a stream near Red Bank, New Jersey. It was near here that the first pair of fishes on which the earlier studies were based had been obtained, so that the present ones should be strictly comparable and may easily bear a close family relationship to the former. Judging from their size it is inferred that the present six fish had never spawned before and presumably were only a year old.

Reproductive Schedule.

Pre-spawning Behavior.

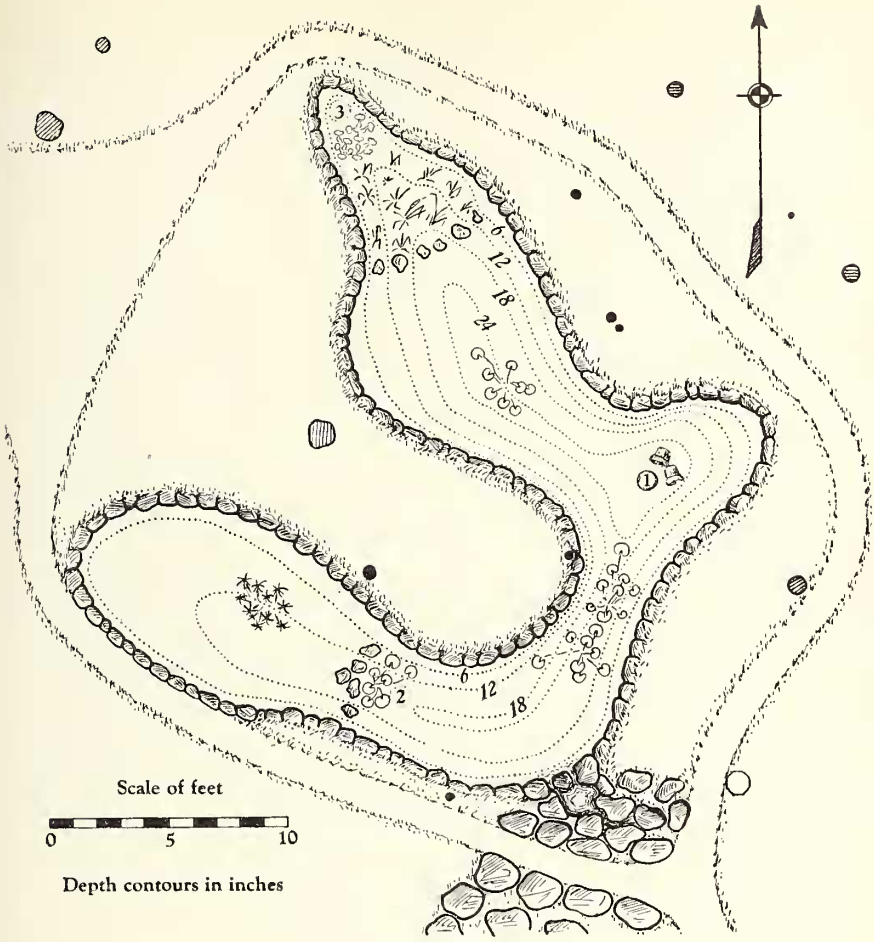
Reproductive activity put in its appearance gradually. It was first noticed that the fish became more active and tended to aggregate at times near the surface or near the shore line. This would be alternated with rooting around all over the pool as though nesting sites were being sought. Insofar as six fish are able to form an aggregation the behavior of these groups was decidedly like that of the supposed pre-nuptial behavior described for *Ameiurus natalis* by Pearson & Miller (1935). After this had gone on for a time, the fish began to show slight injuries as a result of their activities.

Nest Construction.

Gradually the rooting process became more and more intense until the fish had the pool in such a state that visibility was seriously restricted. Although what had been thought to be adequate nesting sites had been provided by the various rocks which held the sand in place, the fish seriously damaged the planting arrangements. These sand breaks are indicated in Text-figure 1 in the two main arms of the pool, only the protruding portions of the rocks being shown. A potted water lily was rooted out of its pot, the pot cleaned completely of all earth, although allowed to remain in a standing position. This was in the face of two identical empty pots laid on their sides especially for the fish not six inches from the other. See the northeast corner of the pool, Text-figure 1. The first pair to spawn used this standing flower pot. With unexpected good fortune it developed that of the six fish placed in the pool three pairings resulted.

The second pair selected a site at the base of another lily pot without disturbing it while the third selected the shallowest and most restricted cove in the entire shore line. The nests are indicated as "1," "2" and "3" in Text-figure 1.

Accustomed to catfishes of this genus and especially of this species spawning in rock cavities, old tin pails, under overhanging logs, roots and so forth, the form of the second two nests came as a surprise. Photographs of typical nests of *Ameiurus nebulosus* are shown by Breder (1935). These were taken in aquaria, as such nests in a wild state are almost impossible to photograph because of their positions. Gill (1907) published an idealized drawing of a nest of this species unlike any seen by the writer or apparently by others. Of this Breder (1935) wrote, "Gill's (1907a) drawing of an *Ameiurus* nest (ideal) is not like any described in the literature or seen by the author, but more nearly resembles a centrarchid nest." His figure is



Text-figure 1.

Sketch map of the pool in which the present studies were made. The numbers 1, 2 and 3 indicate the sites of the three catfish nests. The contour lines indicate the depth of water to the present bottom of sand and leaves. The underlying concrete, below the 12″ contour, is in most places at least a foot deeper. The aquatic vegetation, *Cyperus*, *Nymphaea*, *Typhia*, *Sparganium* and *Eichhornia*, are indicated by appropriate symbols. The immediately surrounding tree trunks are indicated as follows: Locust—black, Plum—horizontal lines, Cherry—diagonal lines, Pear—vertical lines. Footpath around margin of pool indicated as grass edging.

here reproduced as Text-figure 2. Actually it could well represent an idealized condition of the second two nests under discussion, and if sunfish had been in the pool the structures would have undoubtedly attributed to those fishes. Our nests differ from Gill's drawing only in the species of the vegetation surrounding them, a matter in which the fish could exercise small selection. Plate I shows the third nest and clearly indicates the nature of the construction. It was impossible to obtain a good photograph of the second nest because of the greater depth of water in which it was situated and the lingering turbidity from the earlier rooting period.

Text-figure 2.
Catfish (*A. nebulosus*) on nest (Ideal). After Gill (1907), including caption.

Attention to Eggs.

The first nest was placed in such an awkward position as to make normal attention peculiarly difficult for the parent fishes. At the bottom of a small flower pot of less diameter than the length of the fish, the attending parent was forced either to coil itself in too tight a circle for a catfish or stand free in the water at an angle. The latter position was used almost exclusively. This required continuous active swimming on the part of the parent during the entire incubation period. Occasionally it would attempt to coil itself down over the eggs and beat them with its ventral fins. This could scarcely be accomplished and was not tried very often. Thus it appears that this typical catfish activity is not vital to the hatching of the eggs, as this nest produced a large brood. The fish for most part contented itself with fanning the eggs with the tip of the tail as is indicated in Text-figure 3. Here, too, photography was impossible because of the reasons already mentioned.

In the other two nests, which were not constricted in any such way, the attendant parent continually made use of the ventral fins. This behavior

differed from that described by Breder (1935) only in that the motion involved somewhat similar motions of the pectoral fins while the entire fish rocked slightly. As the pectorals were usually over the edge of the egg cluster and the ventrals over its middle the latter supplied most of the effective agitation, as is indicated in Plate II. This was so violent that in the third nest the mass of eggs became broken up into several smaller clusters before hatching. Thus loosened from the ground the eggs were driven against the rim of the nest where they hung while they received only the benefits of the currents produced by the fish which was still working in the center of the nest where the eggs had been originally situated. When the barbels of the parent came in contact with such a cluster of eggs the fish would show signs of agitation but made no effort to return them to the nest proper. The movements of the ventral fins alone in a nest built in a rock cavity as described by Breder (1935) and the present rocking of the entire fish would seem to be purely a mechanical circumstance. Without the rocks on which to steady itself the fish naturally is thrown from side to side by the action of the ventral fins, or, looked at the other way, in an open nest there is no inhibition to more violent activity. In the light of the specialized pelvic musculature of this group of fishes as discussed by Shelden (1937), the activity is certainly primarily of pelvic origin.

The cluster of eggs in the second nest was not broken up as in the third, but remained intact until hatching.

Although the sexing of these fish in a pool is not easy, it is thought that the female did all of the incubating in each case. Individuals could be easily recognized since each had some slight scar that was obtained during the courtship activity. A white crescent across the head of the attendant parent of the third nest, which may be seen in Plates I and II, marked that individual from all the rest. Text-figure 3 indicates the conditions in the first pair. At least, then, one individual did all the incubating and before the eggs hatched apparently never left the nest. Fingers, sticks and so forth introduced in the nest would be faced with open mouth, seldom bitten but frequently butted out of the nest.

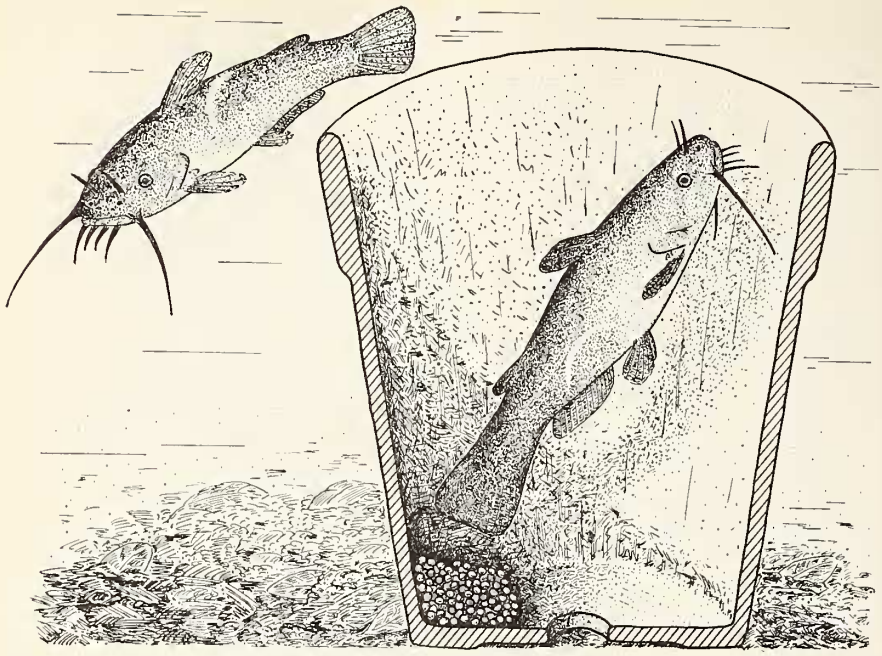
In the case of the first nest, the second parent continually circled the flower pot in a circle with a diameter of about three feet, as if a guard patrolling a circuit. For most part the barbels were held distinctly forward when engaged in this activity, as is indicated in Text-figure 3. In the case of the other two there was no such evident cooperation. The alternate parent of the second nest was once seen to approach the nest but was vigorously driven off by the attendant. This fish, however, was never seen out of the arm of the pool that held its nest, but this may be due to merely being held in the one arm, as any near approach to the first nest resulted in the active resentment of the patrolling parent of that nest.

The alternate parent of the third nest was found for most time resting in the nearby bulrushes. Like that of the second it was prevented from wandering far by the position of the first nest.

It may be noted from Text-figure 1 that the selection of depths varied greatly but the nests are as far apart as they could well be. Each was definitely out of sight of the others. The fact that the southwest arm in its upper reaches was not used may be attributed to the fact that its large shallow area was relatively unprotected with plants as compared with the more abrupt shallowing and heavy planting of the northwest arm. Likely the proximity of deep water and vegetation has a bearing on this selection.

Family Relationships.

After hatching, the young of the first nest, when able to swim up out of the flower pot, were attended attentively by both parents very much after the fashion of those discussed by Breder (1935). The parent of each of the



Text-figure 3.

The nesting behavior of pair number 1. The light curved marks on each fish were received in the courtship and spawning procedure and served as identification marks. The attitudes shown of the two parents were characteristic of this pair. The flower pot is eight inches across the top.

other nests which did not incubate was never seen to take as much notice of its young as did that of the first. One of the purposes of this study was to determine if possible how families were controlled in this species. When the young of the first nest were moving about in a school attended by both parents, the third nest still contained only partly pigmented larvae not yet able to leave the nest. Those in the second nest were somewhat more advanced. The following description of what transpired between the first and third family which was observed in full goes far to illuminate the relationship between parent and offspring in this species.

When once the first family approached the third nest the following activity ensued. On the sight of the approaching large fish the attendant at the nest became agitated and swam rapidly in small circles while the parents with their brood were poking along behind but over the rear of their group. A few of the vanguard of the young school apparently sighted the nesting fish, made more evident by its increased activity. These immediately swam to it, as they ordinarily do to their parents when they increase their activity. Others following in the mass of the school and naturally more influenced by their fellows nearby did not follow these outriders. The true parents at this point apparently became aware that something unusual was taking place and they in turn became agitated with the result that their young flocked to them and the whole group retreated in the opposite direction leaving about half a dozen young with the other fish. The entry of these larger and darker individuals into the nest caused the attendant to become further agitated. It turned and faced first one and then another of the intruders as they tried to nestle under it and wedge into the

pack of smaller fishes. Finally they were accepted and remained there until her own brood was large enough to swim freely.

The second nest had caught some young also, at an earlier time, but it was not understood how this took place until the above observation was made. The sequence of these various items is given in tabular form in Table I. When finally the broods of numbers two and three left the nests they carried with them some of the slightly larger young of number one which could still be clearly distinguished from their brothers and sisters by adoption.

Although the three families could not be under continual observation it is clear that they soon rapidly became mixed and shortly after broke up as distinct schools. At one time the first spawning parents gathered

TABLE I.

Schedule of events in reproducing *Ameiurus*.

Dates	*Pair Number*			*Events*
	1	2	3	
June 12				Excavating and rooting period for all.
13				Water lily uprooted from pot by Pair #1.
14				
15				
16				
17				
18				
19				
20				
21				
22	*(E)*[1]			
23				
24	E			Eggs present—Pair #1.
25				
26				
27		E		Eggs present—Pair #2.
28				
29	*(H)*		E	Eggs present—Pair #3.
30				
July 1				
2				
3	H			Eggs hatched—Pair #1.
4	L	H		Eggs hatched—Pair #2. Left nest—Pair #1.[2]
5				
6			H	Eggs hatched—Pair #3.
7		W		Young of #1 in nest #2.
8			W	Young of #1 in nest #3.
9		L		Young left nest (in part)—Pair #2.
10				
11			L	Young left nest—Pair #3.
12				
13				Schools of young completely mixed.
14				Disintegration of family schools from here on.
Aug. 20				Pair #1 still gives some slight attention to a wandering young one when it approaches.
26				Parental solicitude fully ceased.

[1] Probable true dates indicated in italics in parentheses. Observations in Nest No. 1 extremely difficult because of position and depth.
E—Eggs present.
H—Eggs hatched.
L—Left nest.
W—In wrong nest.

[2] Pair #3—Egg cluster broken into small bits.

what appeared to be all the young fish into one large school. This apparently took place because of the far greater attentions that this pair bestowed upon its young. The attentions of the other two pair when the young were off the nest was at best desultory and interspersed with what seemed to be renewed courtship activities.

The dates of egg-laying, hatching and nest-leaving in nests 2 and 3 as given in Tables I and II are accurate, but due to the position of nest 1 and the consequent difficulties of detailed study, the actual dates of deposition of ova and their hatching are uncertain. Corrected dates, as based on what one would expect from the behavior of the others, are given in parenthesis and italics.

TABLE II.

The duration of the nesting period in *Ameiurus*.

Pair of fish[1]	*Date of egg laying*	*Days to hatch*	*Days to swim*	*Total days in nest*	*Water depth in inches*	*Mean temp. °C*
A 1931	Aug. 18	6	10	16	48	21.1
A 1933	July 15	10	16	26	48	21.1
A 1933	Aug. 13	9	—	—	48	21.1
B 1934	July 5	6	7	13	48	23.3
1 1939	June 24 (*22*)[2]	9 (*7*)	1 (*5*)	10 (*12*)	28	20.8
2 1939	June 27	7	5	12	16	20.8
3 1939	June 29	7	5	12	7	20.8
Mean	July 15	8—	7+ (*8*)	15 — (*15+*)	35 —	21.3 —
Maximum	Aug. 18	10	16	26	48	23.3
Minimum	June 24 (*22*)	6	1 (*5*)	10 (*12*)	7	20.8

[1] Original data on lettered nests prior to 1939 is given by Breder (1935).
[2] The italic numbers in parentheses indicate values corrected according to the estimates in Table I.

DISCUSSION.

From the evidence of the present study it would appear clear that *Ameiurus* basically undertakes to build a saucer-shaped nest similar to, if not indistinguishable from, those of the Centrarchidae. The reason that it is seldom seen as such is because of the proclivity of the species to seek out cavities which inhibit the full expression of the circular form. When, however, a nest is built in the open it takes on a most sunfish-like appearance.

The differences between the usual nests of these two vastly different fishes would seem to be definitely referable to the basic differences in the reaction of the Ameiuridae and Centrarchidae to light. Since the sunfishes normally seek the sunniest spots for their nests and consequently the most open places, it is natural that their nests are not frequently distorted from the circular by large obstructions, as is discussed by Breder (1936), and conversely since catfish are very negatively phototropic it follows that they seldom build in open places.

How, then, is it that in the present study two pairs of catfish built in relatively open places and all three were unprotected above? The answer to this would appear to be that the amount of shading of the pool was such that the fish were not especially driven to seek the shadows of overhanging objects. The spotting of the trees in Text-figure 1 gives only a meager indication of the shading, for there is also an amount of tall-growing shrubs

while the southern shore is protected by a fern bank that rises steeply to about eight feet above the water level in a distance of about twelve feet, and there are other trees just outside the limit of the map. Although the light was sufficient to permit the blooming of various *Nymphaea* plants, most of it was slanting and did not penetrate the water too well. The illumination was greatly less than that in the aquaria previously studied. Although bearing in mind that the optical estimation of light intensity is uncertain, the total units of radiant energy on these nests must have been less than that obtained in the aquarium laboratory, for as pointed out by Breder (1935) it was impossible to incubate eggs there unless they were shaded, of which he wrote, "These eggs were found to be as susceptible to daylight as trout eggs, possibly more so, which is certainly not to be unexpected considering the normal positions of catfish nests." In this connection it should be borne in mind that the attendant parent spent much time shading the eggs with its own body.

The actual mechanics of nest building seem to be merely a paddling with the ventral fins and a continual pivoting about on them. The tail movements incidental to this aid greatly in discharging the stirred up detritus from the area of the nest. Thus the catfish nest is not much greater in diameter than the length of the fish, or more properly, the radius about equals the distance from the insertion of the pelvic fins to the tail's tip.

The nests of the sunfishes, on the other hand, about equal the entire length of the fish in their radii. This is due to the fact that these fish, with their differently constituted form and finnage, pivot at their nose or tail tip, depending which way they happen to be facing.

Considering the large number of unrelated fishes that construct more or less circular nest excavations, it would seem that this simple form of effort may well underlie ichthyic nesting generally, coming to the surface again and again in various guises as other conditions permit or demand.

The selection of nesting sites, as already mentioned, seems to have scant reference to depth. General proximity to shelter, in the form of plants or deeper water, and the avoidance of neighbors would seem to be much more important.

Although it was found that these eggs could not be hatched artificially without considerable agitation, Eycleshymer (1901) and Breder (1935), clearly they can be hatched with only the circulation supplied by the tail of the parent as with pair number one. Since these were young fish and the resulting egg clusters not too massive, it may be that such is possible only when the central mass is not too remote from the periphery of the cluster.

It has been indicated again in these studies that the catfish essentially incubates the spot where the eggs are laid rather than the eggs themselves, as already discussed by Breder (1935).

The mixing of the young and the difference in attitude of the parents confirms the observations of Eycleshymer, (1901), Kendall (1910) and Breder (1935), all of whom described considerable variation from one family to another. Fowler (1917) mentioned variation in the choice of nesting sites, mentioning depths ranging from several feet to a few inches. He further wrote, "Though only a few nests were noticed in a restricted area, sometimes a dozen or more may be found on one shoal and close to one another." Such crowding would suggest a dearth of suitable breeding areas somewhat analogous to that discussed for the Centrarchidae by Breder (1936). Fowler further noted, "Frequently the fish take advantage of any objects, such as logs, rocks, etc., for sheltering the nest." This would certainly indicate that he had familiarity with unprotected nests, but he does not amplify it further. He also mentions that the eggs are deposited at intervals. In all cases of which we have personal knowledge these

intervals are short and occupy a few hours at most, giving in effect a single clutch of eggs. A later and separate spawning may sometimes take place.

So far as it was possible to determine, a single parent, in the present studies, was responsible for each nest. In the aquarium catfishes previously studied both parents incubated and looked after the young and many times in the field two attendants to broods of young have been noted, although also many broods have been seen with a single adult. It is interesting to note that in the present studies only one parent incubated where a nest was built in the open. Since this was presumably the first time that these fishes spawned, it may be that the full details of parental care do not find their complete expression until the fishes have had some experience. In this connection it may be noted that the aquarium studies were all based on much larger and older fishes.

Table II gives the important dates and time in the series of nests studied together with the maximum, minimum and mean conditions. It will be noted that there are marked variations even under closely similar conditions and in some cases in the same pair of fish.

One is tempted to think of catfish in seeking shelter for their nests as somewhat of a protection from various enemies. When it is recalled that sunfish seek the reverse positions, often in the same ponds, one wonders how significant such protection is, especially as catfish seem to be able to raise successful broods in sunfish-like localities. In this connection it is interesting to note that it was earlier found that the common goldfish could not be kept in this pool because of visitations of kingfishers from a nearby creek. It thus may actually be that catfish seek hollows for spawning merely as a result of their normal avoidance of bright light without imputing any survival value that such behavior might conceivably hold.

The early and thorough mixing of the broods found to occur during the present studies may well have been intensified by the exposed positions of two of the nests. Well hidden nests would seem to be less likly to be entered by the young of other broods. Also if they did it would be less readily observed. Since a good crop of young fish were derived from these nests it would be difficult for this and for theoretical reasons to impute any survival value, positive or negative, to this mixing of families when conditions permit or force it.

Summary.

1. Although usually nesting in natural cavities, *Ameiurus nebulosus* may at times construct saucer-shaped nests not unlike those of centrarchids. The extent of shading in the spawning area may be associated with this.

2. Eggs can be successfully incubated without recourse to the use of the ventral fins for agitating them, tail waving being adequate for the purpose.

3. Broods of clearly different sizes in nearby nests may become inextricably mixed from the time they first are able to swim.

4. There is considerable variation between one pair and another in regard to all the phases of breeding activity.

Bibliography.

Breder, C. M., Jr.

1935. The Reproductive Habits of the Common Catfish, *Ameiurus nebulosus* (Le Sueur), with a Discussion of their Significance in Ontogeny and Phylogeny. *Zoologica*, **19** (3):143-185.

1936. The Reproductive Habits of the North American Sunfishes (Family Centrarchidae). *Zoologica*, **21** (1):1-48.

EYCLESHYMER, A. C.
1901. Observations on the Breeding Habits of *Ameiurus nebulosus*. *Amer. Nat.*, **35**:911-918.

FOWLER, H. W.
1917. Some notes on the breeding habits of local catfishes. *Copeia*, (42) :32-36.

GILL, T. N.
1907. Parental Care among Fresh-water Fishes. *Rept. Smithsonian Instit. for 1905*, (1688) :403-531.

KENDALL, W. C.
1910. American catfishes; habits, culture and commercial importance. *Rep't. U. S. Comm. Fisheries, 1908*:3-39.

PEARSON, J. F. W. & MULLER, E. M.
1935. Aggregations of *Ameiurus natalis erebennus* Jordan, the Florida fresh-water Catfish. *Ecology*, **16** (1) :123-125.

SHELDEN, F. F.
1937. Osteology, myology and probable evolution of the Nematognath pelvic girdle. *Ann. N. Y. Acad. Sci.*, **37** (1) :1-96.

EXPLANATION OF THE PLATES.

Plate I.

The nest of pair number 3. The sunfish-like nature of the construction is well indicated. The spawning mark, on the head of the attending fish, may also be seen.

Plate II.

The attendant of pair number 3 at the moment of beating the eggs with the ventral fins. Note their spread position. At most other times they are hidden under the body. The water striders on the surface were given no attention, but the snail crawling into the nest caused some agitation but no definite action.